

Some Factors Effecting Algal Consumption in Subarctic Ephemeroptera, Plecoptera and Simuliidae

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Summary. Some of the factors influencing algal consumption in the mayflies *Leptophlebia nebulosa*, *Cinygmula tarda*, *Baetis foemina* and *B. cf. bicaudatus*, the plecopterans *Arcynopteryx signata*, *Nemoura cinctipes* and *N. oregonensis* and in the dipterans *Simulium arcticum*, *S. venustum* and *S. decorum* were investigated between June 1975 and June 1976 in several streams in the Canadian subarctic. Algae represented up to 65% of the gut contents of *L. nebulosa* but only 0–8% in the other mayflies. They were important in the plecopterans (85–90%) but less so (2–13%) in the simuliids. Most of the interspecies variability in algal consumption could be explained in terms of food availability. This factor was in turn dependent on the density and attachment characteristics of the flora and the strength of their cell wall. Feeding intensity in most species was low between October and April, reaching its peak in July and August. From 51 to 83% of intraspecies feeding variability was due to changing temperature, followed in importance by water velocity in the dipterans and food availability in the mayflies. All species in this latter group ceased feeding in the final instar stages.

Introduction

The importance of algae in the diet of aquatic insects is highly variable. It depends to a large degree on the species of animal (Bengtsson, 1925; Wissmeyer, 1926; Monakov, 1972; Anderson and Grafius, 1975), its age and size (Brown, 1961; Winterbourn, 1971; Anderson, 1974), habitat (Hall and Pritchard, 1975), time of day (Gerson, 1974) and species of algae (Brown, 1961; Moore, 1975). In some habitats, particularly eutrophic temperate zone streams, algae may form the bulk of the gut contents (Cummins, 1973) while, in more oligotrophic areas, they may be of minor consequence (Hanna, 1957; Minshall, 1967).

Comparatively little is known about the role of algae in the diet of aquatic insects in subarctic streams. Thus the purpose of this study was to describe and try to explain seasonal changes in the quantity of ingested microflora

in several species of Ephemeroptera, Plecoptera and Simuliidae. Collections were made from a number of streams situated in northwestern Canada.

Materials and Methods

Samples of the mayfly *Leptophlebia nebulosa* Banks and the blackflies *Simulium arcticum* Mall. and *S. venustum* Say were made monthly at Boundary Creek (Lat. 62°35' Long. 155°10'), a tributary of Great Slave Lake. Twenty representatives of each species were normally captured near midday with a Surber sampler. They were returned immediately to the laboratory for analysis (Moore, 1975). Water temperatures in Boundary Creek, which is 5 km long and 10 m wide, were at or near 0°C from October to April rising to 12°C in August. Water velocity over the collection sites averaged 25–45 cm/s rising to 100 cm/s in May. The rocky substrate was partly covered with extensive growths of algae (mainly *Bulbochaete* sp. and diatoms) where *L. nebulosa* could be found. The occasional bare patches of rock supported *Simulium* spp. Collections of attached and planktonic algae (i.e. potential food sources) in this and the following streams were made as outlined earlier (Moore, 1976). Additional physico-chemical and biological data on Boundary Creek are available elsewhere (Moore, 1977a).

Collections of blackfly larvae (*Simulium arcticum*, *S. venustum*, *S. decorum* Walk.) were also made from Baker Creek (Lat. 62°31' Long. 114°21'), another tributary of Great Slave Lake. The material was taken every 2 weeks and analyzed as outlined preceding. Baker Creek, measuring 5 km long and 3 m wide, was ice covered from April to October with temperatures rising to 17°C in summer. Although water velocity over the rocky substrate normally averaged ca. 20 cm/s, it exceeded 100 cm/s during the period of high run off (May).

Collections of the mayfly nymphs *Cinygmula tarda* McD., *Baetis foemina* Say and *B. cf. bicaudatus* Dodds were made twice (August and December 1975) in the Flat River (Lat. 61°58' Long. 128°14'), which is situated in the Selwyn Mountains near the Yukon. Additional samples of the plecopterans *Arcynopteryx signata* Hagen, *Nemoura cinctipes* Banks and *N. oregonensis* Claassen were taken in December, these being absent from the Flat earlier in the year. The animals were collected from rocks 2–10 cm in diameter with extensive algal growths occurring at the substrate surface. The Flat is a large river, measuring about 250 km long, 10–15 m wide with discharge ranging from 15 to 600 m³/s. During August water temperature and current speed were 5°C and 20 cm/s, respectively, falling to 0°C and 10–20 cm/s in December.

Results

Leptophlebia nebulosa

A highly diverse and plentiful algal flora was found in *Leptophlebia nebulosa*, as exemplified by the August and December data (Figs. 1 and 2). Fragments of *Bulbochaete* were invariably predominant in the gut regardless of size class or time of year. Unicellular diatoms (*Achnanthes minutissima*, *Nitzschia palea*, *Navicula* spp.), chlorophytes (*Scenedesmus denticulatus*) and chrysophytes (*Dinobryon divergens*) comprised a highly variable but usually important part of the diet. In the environment, *Bulbochaete* was also always predominant and formed filaments up to 30 cm long (Fig. 1). Considerable numbers of diatoms also occurred on the rocks, with the Chlorophyta and Chrysophyta being found in only small numbers. While most species were consumed in proportion to their abundance in the environment, ingestion of *Cocconeis placentula* was limited.

While 40–60% of ingested *Bulbochaete* was fragmented, the cell wall of

Table 1. Percentage of algae found in the anterior 20% and the posterior 20% of the gut of *Leptophlebia nebulosa* and *Simulium arcticum* which retained the colour of their chloroplasts

| Species | August | | December | |
|--|-------------|-----------|-------------|-----------|
| | Anterior | Posterior | Anterior | Posterior |
| <i>Leptophlebia nebulosa</i> | | | | |
| <i>Achnanthes minutissima</i> Kz. | 73.0 | 1.5 | 38.4 | 35.3 |
| <i>Bulbochaete</i> sp. | 93.0 | 47.5 | 74.3 | 77.2 |
| <i>Dinobryon divergens</i> Imhof | 57.0 | 10.1 | 19.2 | 0.7 |
| <i>D. suecicum</i> v. <i>longispinum</i> Lemm. | 82.3 | 15.0 | 29.8 | 6.6 |
| <i>Navicula cryptocephala</i> Kz. | 57.0 | 1.0 | 62.0 | 57.3 |
| <i>N. radiosa</i> Kz. | 60.5 | 7.9 | 71.5 | 70.4 |
| <i>Nitzschia palea</i> (Kz.) W. Sm. | 72.3 | 9.2 | 39.2 | 44.3 |
| <i>N. subtilis</i> (Kz.) Grun. | 51.9 | 5.5 | 44.4 | 29.9 |
| <i>Simulium arcticum</i> — Boundary Creek | | | | |
| <i>Ankistrodesmus falcatus</i> (Corda) Ralfs | 95.7 | 90.0 | 100.0 | 100.0 |
| <i>Dactylococcopsis fascicularis</i> Lemm. | 100.0 | 100.0 | 100.0 | 100.0 |
| <i>Dinobryon bavaricum</i> Imhof | 73.5 | 5.3 | 55.9 | 20.0 |
| <i>D. borgei</i> Lemm. | not present | | 60.5 | 17.6 |
| <i>D. divergens</i> | 59.0 | 1.0 | 20.5 | 7.2 |
| <i>D. sertularia</i> Ehr. | 40.0 | 0.0 | 73.3 | 5.5 |
| <i>D. suecicum</i> v. <i>longispinum</i> | 92.3 | 0.0 | 35.7 | 0.0 |
| <i>Merismopedia punctata</i> Mey. | 100.0 | 100.0 | 95.0 | 93.5 |
| <i>Simulium arcticum</i> — Baker Creek | | | | |
| <i>Ankistrodesmus falcatus</i> | 100.0 | 100.0 | 90.0 | 89.3 |
| <i>Merismopedia tenuissima</i> Lemm. | 100.0 | 100.0 | 100.0 | 100.0 |
| <i>Oscillatoria tenuis</i> Ag. | 100.0 | 100.0 | not present | |
| <i>Scenedesmus denticulatus</i> Lag. | 100.0 | 95.5 | 87.3 | 85.7 |
| <i>S. quadricauda</i> (Turp.) Bréb. | 100.0 | 95.0 | 80.5 | 82.3 |

all unicellular algae remained intact during passage through the gut. During summer, the chloroplasts of all chrysophyte and most diatom species had disappeared after transport to the end of the gut (Table 1). The cellular content of the fragmented *Bulbochaete* similarly disappeared but, in the case of entire cells, breakdown failed to occur. During winter only the chrysophyte species were digested. The maximum length of organism found in the 8–10 mm size class was 125 µm with corresponding values for 6–7 and 4–5 mm animals being 96 and 87 µm respectively.

The total number of ingested cells was usually high, particularly in summer (Fig. 2). Large (8–10 mm) specimens contained 27×10^3 cells while 5–6 mm specimens had 5×10^3 cells. Algae represented 45–64% by volume of the gut contents in summer and 10–20% in winter. This high consumption was well correlated with the continual presence of large numbers of algae in the environment (i.e. 1×10^6 cells/cm² in summer and 0.5 cells/cm² in winter).

Feeding intensity fluctuated greatly with time of year irrespective of size class (Fig. 2). Multiple regression analysis of 4 independent variables indicated that temperature accounted for about 83% of the feeding variability followed

in order of descending importance by food availability, water velocity and changing daylength (Table 2). No food was found in the gut of mature animals, i.e. those on the verge of transformation to the subimago stage.

Apart from algae the only other items occurring in the gut were detritus and sand grains. The latter particles were usually small, i.e. $< 10 \mu\text{m}$, but occasionally reached 25–35 μm dia irrespective of size of animal. In the environment, many particles exceeded 100 μm . An episammic flora was not associated with the sand grains.

Simulium spp.

Algae, detritus and sand grains were found in the gut of *Simulium arcticum* collected from Boundary Creek. The most frequently ingested species during the summer was *Dinobryon sertularia* but was replaced with *D. suecicum* var. *longispinum* and *D. borgei* in the winter. The Chlorophyta (mainly *Ankistrodesmus falcatus*) the Cyanophyta (*Merismopedia punctata*) and the Pyrrophyta (*Peridinium cinctum*) taken together always represented $< 10\%$ of the gut contents. Selection for or against particular species was not evident (Fig. 3).

The cell wall of all phytoplankton remained intact during passage through the gut. The Chlorophyta and Cyanophyta were never broken down, as illustrated through the presence of pigment at the end of the the gut (Table 1).

Table 2. Multiple regression analysis of some factors influencing algal consumption in *Leptophlebia nebulosa* and *Simulium arcticum*. r = correlation coefficient; b = slope constant; MR^2 = accumulated variation (%) of the dependent variable accounted for by the step-wise addition of the independent variables

| Independent variable | Rank | r | b | MR^2 |
|--|------|-------|--------|--------|
| a) Dependent variable: Algal numbers in <i>Leptophlebia nebulosa</i> | | | | |
| Temperature | 1 | 0.91 | 1.248 | 83.4 |
| Food availability | 2 | 0.64 | 2.157 | 87.3 |
| Water velocity | 3 | 0.09 | 0.039 | 89.8 |
| Daylength | 4 | 0.79 | 0.459 | 91.9 |
| b) Dependent variable: Algal numbers in <i>Simulium arcticum</i> from Boundary Creek | | | | |
| Temperature | 1 | 0.72 | 0.079 | 51.4 |
| Water velocity | 2 | -0.15 | -0.021 | 64.4 |
| Day length | 3 | 0.55 | 0.022 | 64.9 |
| Food availability | 4 | 0.67 | -0.017 | 65.4 |
| c) Dependent variable: Algal numbers in <i>Simulium arcticum</i> from Baker Creek | | | | |
| Temperature | 1 | 0.81 | 0.058 | 64.9 |
| Water velocity | 2 | -0.22 | -0.026 | 67.9 |
| Day length | 3 | 0.55 | 0.026 | 68.4 |
| Food availability | 4 | 0.39 | -0.012 | 68.6 |

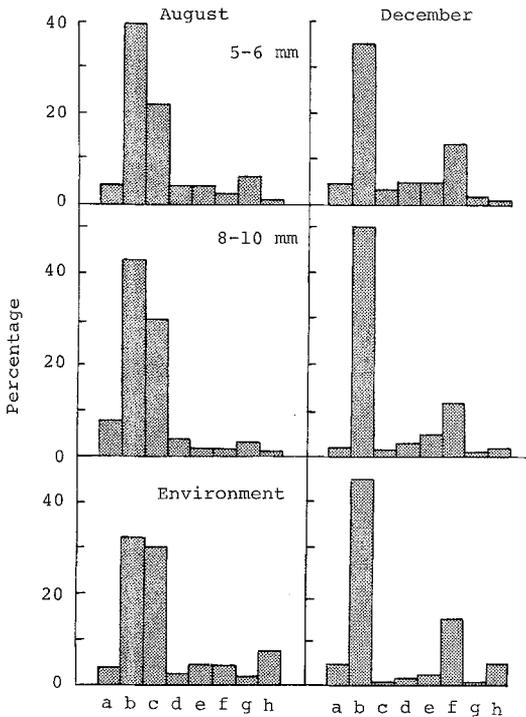


Fig. 1. Relative abundance of common algae in the gut of *Leptophlebia nebulosa* of different length collected from Boundary Creek. a *Achnanthes minutissima*, b *Bulbochaete* sp., c *Dinobryon divergens*, d *D. suecicum* var. *longispinum*, e *Navicula cryptocephala*, f *N. radiosa*, g *Nitzschia palea*, h *N. subtilis*

The Chrysophyta were, however, easily digested, even in winter. The maximum length of plant found in the >7 mm and 3–4 mm size classes were 102 and 62 μm respectively while the corresponding minimum values were 10 and 9 μm .

The total number of ingested cells fluctuated greatly depending on season and animal size (Fig. 4). Large (>7 mm) specimens, for example, contained 8×10^4 cells in summer but less than 5000 in winter with corresponding values for 3–4 mm specimens being 15,000 and ca. 100. In terms of volume, algae represented 1.2–4.5% of the total gut contents. In the environment, phytoplankton density changes were quite irregular with maximum densities (3×10^4 cells/l) occurring in June and October. During the winter, standing crop values seldom exceeded 1000 cells/l. Multiple regression analysis indicated that temperature was the most important factor influencing *Simulium* feeding, followed by changing water velocity and daylength (Table 2).

Simulium venustum occurred in Boundary Creek only between June and October. Since the feeding biology of this species was similar to that outlined preceding, a further account will not be given.

The most frequently encountered algae in the gut of *Simulium arcticum* collected from Baker Creek were the Chlorophyta *Ankistrodesmus falcatus*, *Scenedesmus denticulatus* and *S. quadricauda* and the Cyanophyta *Merismopedia tenuissima* and *Oscillatoria tenuis*. The species composition of the gut contents was similar to that in the plankton. Virtually all ingested microflora retained the colour of their chloroplasts near the end of the gut and their cell walls

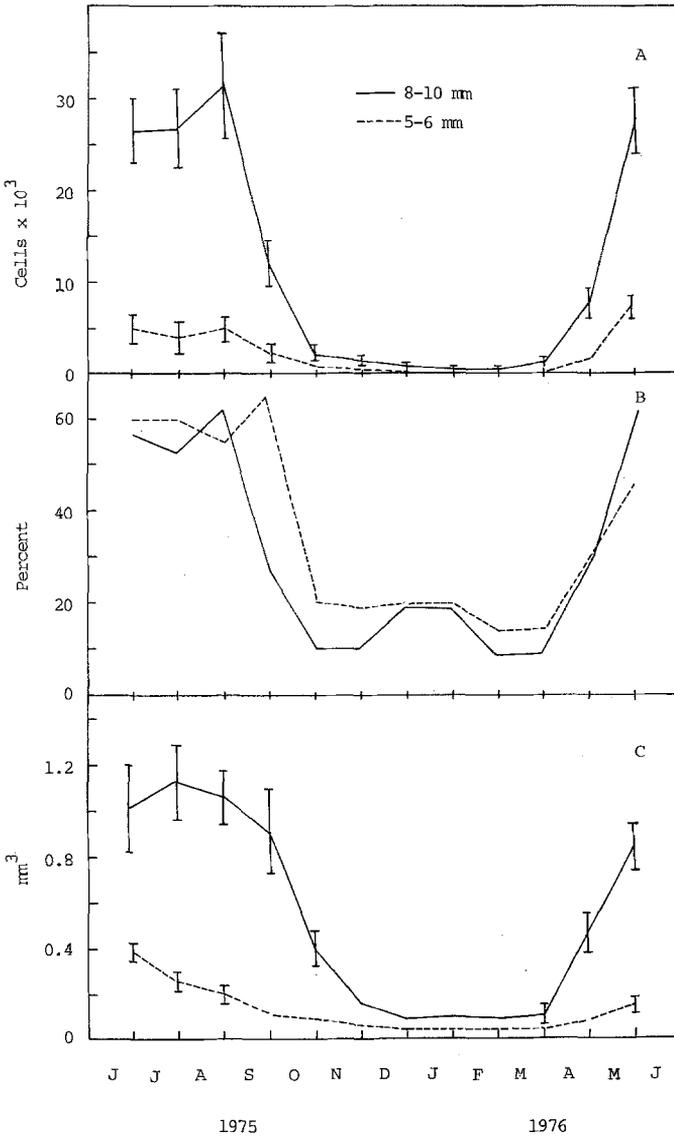


Fig. 2. **A** Changes in the number of algal cells in the gut of *Leptophlebia nebulosa* of different length. Vertical bar represents 95% confidence limits. **B** Changes in the relative contribution of algae to the total volume of the gut contents of *Leptophlebia nebulosa* of different length. **C** Changes in the volume of gut contents of *Leptophlebia nebulosa* of different length

were always undamaged. The longest plant found in the gut of > 7 mm specimens, *Oscillatoria tenuis*, measured 123 μ m while in shorter (3-4 mm) animals, the corresponding value was 80 μ m. Seasonal changes in the quantity of ingested algae paralleled those outlined for Boundary Creek specimens. However, the relative contribution of algae to the gut contents was relatively greater, i.e.

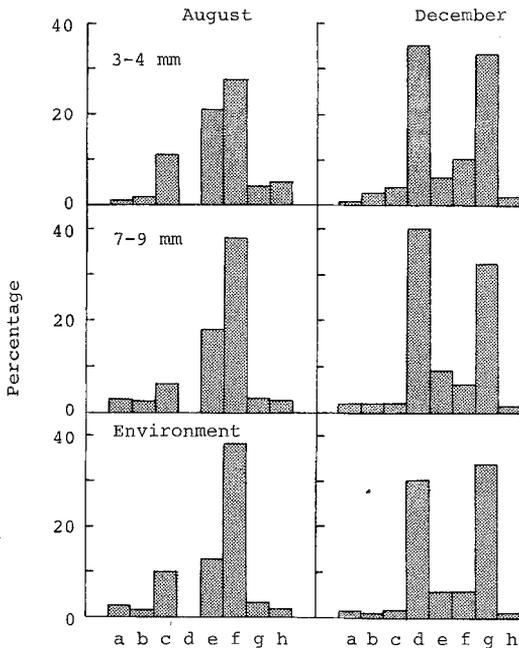


Fig. 3. Relative abundance of common algae in the gut of *Simulium arcticum* of different length collected from Boundary Creek. a *Ankistrodesmus falcatus*, b *Dactylococcopsis fascicularis*, c *Dinobryon bavaricum*, d *D. borgei*, e *D. divergens*, f *D. sertularia*, g *D. suecicum* var. *longispinum*, h *Merismopedia punctata*

5–13%. Temperature was by far the most important factor influencing feeding intensity (Table 2).

Sand grains always occurred in the gut, with the average length of these particles being ca. 10 μm , irrespective of animal size. In the environment many particles exceeded 50 μm . Detritus seemed to make up the remainder of the gut contents and fungus and pollen spores were absent. Since consumption of algae by *S. decorum* and *S. venustum* was identical to that outlined for *S. arcticum*, a further account will not be given.

Cinygmula tarda and *Baetis* spp.

Algae occurred abundantly in the gut of *Cinygmula tarda* collected from the Flat River during August. Specimens measuring 2–6 mm long ingested *Gomphonema angustatum* (Kz.) Grun. and *G. olivaceum* (Lyng.) Kz. with greatest frequency, these 2 species representing 38 and 25% respectively of the flora. *G. angustatum* and *G. olivaceum* were rarer in the epilithon (10 and 8%) being replaced with *Diatoma tenue*, *Achnanthes minutissima*, *Fragilaria vaucheriae* (Kz.) Peters, and *Cymbella ventricosa* Ag. Extensive growths of *Tetraspora lubrica* (Roth) Ag., a filamentous chlorophyte, also occurred on the substrate, but were never ingested.

The total volume of the gut contents of 2–4 and 5–6 mm specimens averaged $0.05 \pm 0.01 \text{ mm}^3$ ($\pm 95\%$ confidence limits) and $0.4 \pm 0.1 \text{ mm}^3$ respectively. Algae

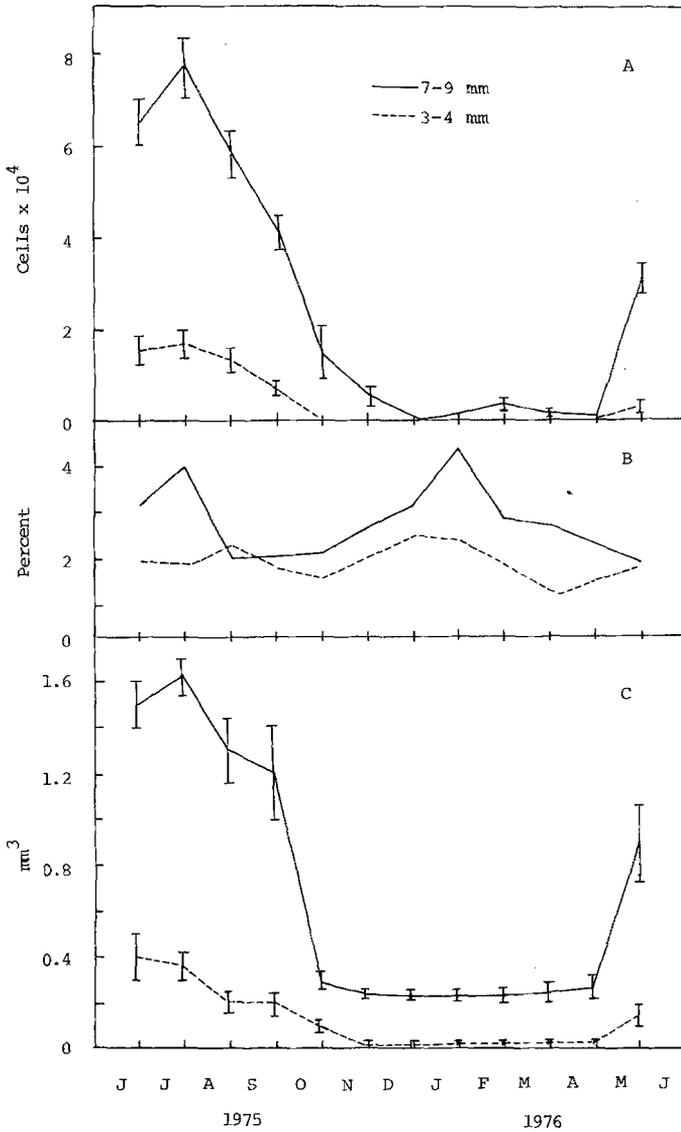


Fig. 4. **A** Changes in the number of algal cells in the gut of *Simulium arcticum* of different length collected from Boundary Creek. **B** Changes in the relative contribution of algae to the total volume of the gut content of *Simulium arcticum*. **C** Changes in the volume of gut contents of *Simulium*

accounted for $8 \pm 2\%$ and $6 \pm 1\%$ of these values, with the remainder consisting of small ($< 10 \mu\text{m}$) sand grains and detritus. Nymphs longer than 6 mm, i.e. those on the verge of transformation to the sub-imagio stage, and all those collected during December had not recently fed.

While *Baetis foemina* and *B. cf. bicaudatus* contained considerable amounts of ingested detritus and small sand grains during August and December, algae

were not observed in any portion of the gut. As in the other mayflies, specimens nearing transformation had apparently stopped feeding.

Arcynopteryx signata and *Nemoura* spp.

The December collections of *Arcynopteryx signata* (15–20 mm long), *Nemoura cinctipes* (4–5 mm) and *N. oregonensis* (4–5 mm) yielded large amounts of ingested algae. The predominant species in all 3 animals was *Diatoma tenue*, accounting for $65 \pm 5\%$ of the flora, followed in order of descending importance by *Ceratoneis arcus* Ehr. ($21 \pm 2\%$) and *Diatoma hiemale* var. *mesodon* (Ehr.) Grun. ($5 \pm 0.7\%$). Extensive growths of *Tetraspora lubrica* covered the entire substrate of the river but were never ingested. Diatoms also occurred abundantly (1×10^5 cells/cm²), the predominant species being *D. tenue*. This plant represented 52% of the flora and was followed by *Ceratoneis arcus*, *Fragilaria vaucheriae* and *Achnanthes minutissima*. Only 40–50% of the 3 animals contained food in their gut. The average volume of the gut contents of *A. signata*, *N. cinctipes* and *N. oregonensis* were 12.1 ± 2.6 , 0.6 ± 0.1 and 0.6 ± 0.1 mm³ respectively with algae representing 88 ± 6 , 72 ± 3 and $87 \pm 6\%$ of these values. The remainder of the gut contents consisted of small (<15 µm) sand grains and detritus.

Discussion

The elevated level of algal consumption in *Leptophlebia nebulosa* parallels the situation in closely related European species (Moon, 1938; Brook, 1955; Popham, 1955). These nymphs scrap organic material from the surface of rocks (Cummins, 1973) where attached algae are often plentiful (Moore, 1976). The inability of *L. nebulosa* to remove *Cocconeis placentula* from the bottom is probably related to the fact that this alga lies much closer (<3 µm) to the substrate than other species. Thus the scraping mechanism passes over *C. placentula*. This feature has also been noted in amphipods, isopods and trichopteran larva (Moore, 1975; Mecom and Cummins, 1964) but not in some Heptageniidae and Chloeonidae (Margalef, 1948). Since *Bulbochaete* sp. was ingested by all sizes of *L. nebulosa*, the relatively thick cell wall of this species does not restrict consumption. In contrast, trichopteran larvae and amphipods have considerable difficulty in utilizing filamentous Chlorophyta (Slack, 1936; Moore, 1975), as also noted for the Ephemeroptera and Plecoptera in the Flat River. Similarly, in certain mayflies, small nymphs are unable to ingest this type of alga while large specimens may depend heavily on it (Brown, 1961).

As only small sand grains were ingested, episammic algae played no part in nutrition, a feature noted for larval lamprey (Moore and Beamish, 1973). In the amphipod *Corophium volutator* large sand grains and associated bacteria are also not ingested (Fenchel, Kofoed and Lappalainen, 1975). The gut contents of several benthic herbivores, e.g. Chironomidae and tubificids (Brinkhurst, Chau and Kaushik, 1972; Davies, 1975), often contain a greater proportion

of organic material than the sediments. Presumably these animals also fail to ingest large sand grains (and associated episammon). The absence of pollen and fungi from the gut of *L. nebulosa* contrasts with herbivorous populations in temperate areas where these components may form a substantial part of the diet (Kaushik and Hynes, 1968, 1971; Bärlocher and Kendrick, 1973a, b).

The incomplete breakdown of ingested algae, as demonstrated through the presence of green coloured chloroplasts near the gut's end, is widespread among benthic and planktonic herbivores (Fryer, 1957; Madsen, 1974; Moore and Beamish, 1973). Since *L. nebulosa* was able to break down most algal chloroplasts during summer, the microflora must have been a major source of energy. The inefficient use of ingested *Bulbochaete* at this time was undoubtedly due to its thick cell wall.

As demonstrated through multiple regression analysis, temperature was by far the most important factor influencing feeding. This feature has also been shown for *Chloeon dipterum* but in *Baetis rhodani* feeding continues throughout both the summer and winter (Brown, 1961). The almost insignificant contribution of food availability to changes in gut content volume was due to the continual presence of a comparatively stable and large amount of organic material on the rocks. The sharp reduction in the amount of algae in the environment during the winter did, however, result in a considerable decline in their contribution to the gut contents. This feature has also been noted in some trichopteran larvae, while in other insects, algal consumptions remains constant throughout the winter (Chapman and Demory, 1963).

Selection for *Gomphonema* spp. occurs in a number of herbivores including amphipods, isopods and molluscs (Moore, 1975; Calow, 1973) as well as in *Cinygmula tarda*. These cells are raised well above the substrate by their stalks and thus easily detached by scraping action. Many other diatoms on the other hand lie close to the bottom, often in crevices and hollows, the most extreme example being *Cocconeis* spp. In some protozoans, both adnate and stipitate algae are not consumed because of the difficulty involved in detaching these plants from the substrate (Moore, 1977b).

The insignificant contribution of algae to the diet of *Baetis foemina* and *B. cf. bicaudatus* is similar to populations occurring in an oligotrophic mountain stream (Pearson and Kramer, 1972) and in England (Brown, 1961). This latter author suggested that algal consumption in *Baetis* depends heavily on food availability. Since, however, the microflora was always abundant in the Flat River, this factor could not have been of major importance in food selection. Presumably *B. foemina* and *B. cf. bicaudatus* fed beneath the substrate surface where algae would be scarce.

Herbivorous plecopteran nymphs generally inhabit streams only during the colder months when algal populations are depressed. Thus consumption of the microflora is highly restricted, with detritus becoming the major dietary item (Hynes, 1941; Brinck, 1949; Jones, 1950; Elwood and Cushman, 1975; Kerst and Anderson, 1975). The highly significant contribution of algae to Plecoptera in the Flat River can therefore be explained in terms of abundant algal growth in winter. In contrast to the work of Hynes (1941), heavy feeding occurred at 0°C. This feature is presumably related to differential metabolic

response to low temperatures (Brown, 1961).

The relatively small contribution of algae to the diet of *Simulium arcticum*, *S. venustum* and *S. decorum* in both Boundary and Baker Creeks, parallels their availability in the environment (Moore, 1977b). Several other closely-related species also consumed relatively little algae (e.g. Chapman and Demory, 1963) whereas in eutrophic areas they were of considerable dietary importance (Puri, 1925; Jones, 1949, 1950; Cummins, 1973). Simuliidae apparently have considerable difficulty in digesting many types of algae, as exemplified by the presence of Chlorophyta and Cyanophyta in the gut with intact chlorophyll. Thus, the microflora were not an important dietary item in the Boundary and Baker Creek populations, a view supported by their small contribution to gut content volume. This trend was even more exaggerated during the colder months when consumption and digestion of algae dropped sharply. As bacteria often contribute significantly to the nutritional requirements of filter-feeding dipterans inhabiting temperate zone streams (Ivlev, 1945; Freedon, 1960, 1964), they should also be important to subarctic/arctic populations. In some filter-feeding animals, however, bacteria cannot support body maintenance despite very high concentrations (Moore and Potter, 1975). Since *S. arcticum*, *S. venustum* and *S. decorum* consumed large quantities of detritus and sand grains, their associated bacterial flora may have also been of considerable nutritional value.

As in the case of *Leptophlebia nebulosa*, feeding intensity in both the Boundary and Baker Creek populations depended primarily on temperature. The Simuliidae were, however, effected to a much greater degree by water velocity. This shift is undoubtedly related to the fact that Simuliidae occur on the surface of stones where there is no protection from adverse current conditions. *L. nebulosa*, on the other hand, has the option of returning to the underside of rocks.

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